On the Direction of the Aqueous Current in the Spiracle of the Dogfish; together with some Observations on the Respiratory Mechanism in other Elasmobranch Fishes. By A. D. Darbishire, Demonstrator of Zoology in the Royal College of Science, London. (Communicated by Professor A. Dendy, D.Sc., Sec.L.S.)

(With 3 Text-figures.)

[Read 2nd May, 1907.]

The observations which I have to record are the outcome of a suggestion made to me by Prof. Dendy that I should find out whether water entered, or came out of, the spiracle in the Dogfish. The point seems simple; yet it is one on which it is impossible to obtain definite information from text-books of zoology.

The observations were begun with Prof. Dendy, at the Royal College of Science, on small Dogfish which had only just hatched; and were continued by me at the Laboratory of the Marine Biological Association at Plymouth, where I occupied the British Association Table. I wish to record my indebtedness to the Staff of the Laboratory at Plymouth for the trouble they took in obtaining fish for me, and to Mr. A. I. Smith, in particular, for his help in my observations.

I shall first give an account of the general mechanism of respiration in *Scyllium canicula*. This account is based on observations of more than twenty Dogfish, which varied in length between 1 and 2 feet. The observations were made partly in the large brick tank with a bottom of shingle and sand, behind the Laboratory at Plymouth; and partly, when closer examination was desired, in a glass vessel, to be described further on.

The results obtained with the just-hatched Dogfish were not conclusive: I shall therefore postpone reference to them until after I have dealt with the respiration as observed in the adult fish.

SCYLLIUM.

Each separate respiratory act in the Dogfish consists of an inspiratory and of an expiratory phase.

The term inspiratory phase may be given to the first phase of the act of respiration, which commences when the whole branchial region begins to expand and ends when this expansion has reached its full extent. Directly this expansion begins (i) the mouth opens slightly, and (ii) the skin forming the outer wall of each gill-slit becomes closely pressed against its corresponding inner wall, evidently as a result of the incipient movement of water towards it. This apposition of the two walls of each gill-slit continues until the branchial region has reached its full state of expansion. The process of expansion can be seen both from above and from below ; and consists therefore in the lowering of the wall of the pharynx as well as in the outward movements of its sides. It has the appearance of being the result of a considerable effort on the part of the fish.

Just before the end of the inspiratory phase the mouth shuts : then the branchial region suddenly collapses, water rushes out of the gill-slits, and the expiratory phase has begun ; and scarcely has it begun before it is at an end, for it takes about half the time occupied by the inspiratory phase.

We must now consider the question of the direction of the water in the mouth and spiracle. In order to determine the direction of the water in these apertures, I placed the Dogfish in 3 to 4 inches of water in a flat-bottomed glass dish. This dish was raised on four corks about 2 inches high ; so that, by placing a mirror below the dish, one could examine the fish from the ventral aspect. The method I adopted for determining the direction of the current in the mouth and spiracle was to gently liberate from a pipette a little finely powdered carmine suspended in sea-water in the immediate proximity of these apertures.

When the mouth opens at the beginning of the inspiratory phase, water is vigorously drawn in : and this inhalation continues so long as the mouth remains open. Water containing carmine which enters the left side of the mouth emerges only from the gills of the left side ; and water entering at the right side emerges only from the gills of the right side. The lumen of the pharynx is, therefore, divided in front of the first gill-slit into two channels which do not communicate with one another. Carmine liberated in front of the middle of the mouth emerges from the gills of both sides, as a result, presumably, of the equal distribution of the cloud of carmine to the two channels.

The carmine sucked in through the mouth does not emerge equally from all the gills ; but in considerably greater volume from the last three, especially from the last one. My attention was first called to this by Dr. Allen, who was watching one of my observations.

Lastly, if carmine is liberated sufficiently near the nostril, the very slightest current, entering it, can be detected.

To turn now to the spiracle. At first sight this aperture seems to give rise to two channels entering the head, a dorsal and a ventral one. The dorsal one is not a channel, but is the spiracular cæcum ; the ventral one is the inspiratory aperture. During the inspiratory phase the inspiratory aperture is open ; but during the expiratory phase it is closed by a valve which extends backwards over it like a curtain, from the anterior wall of the spiracle.

Carmine liberated near the spiracle is vigorously drawn into the inspiratory aperture during the inspiratory phase. During normal breathing there is no expulsion of water from the spiracle, though the faintest outward disturbance in the cloud of carmine caused, possibly, by the shutting of the valve can just be detected. Occasionally, however, the Dogfish clears his spiracle, so to speak, by expelling a considerable volume of water from it. This only happens after a number of trials with carmine, and is evidently a means of ridding the pharynx of unpleasant matter.

The carmine which is drawn into the spiracle emerges from the first three gills, but especially from the first one, or two. It will be remembered that water which entered the mouth emerged from the posterior two or three gills. It seems reasonable to suppose that this difference between the course of the oral and spiracular currents is, in some way, connected on the one hand with a slight difference between the degree of oxygenation of the water composing the two currents (like that between systemic and carotid blood in the Frog), and on the other with that aggregation of the roots of the afferent branchial vessels which affects the first two in *Scyllium*, and the last three as well as the first two in *Raja*.

The observations made on the just-hatched Dogfish at the Royal College of Science were not conclusive, partly because of the smallness of the spiracle, which made it very difficult to determine the direction of the current; and partly because in two of the three youngsters no trace of an ingoing current could be detected, whilst in the third carmine was most distinctly drawn in. Whether this apparent difference between the fish was due to difficulties in observation or to real differences between the fish, I am not prepared to say definitely, though I am inclined to attribute it to the latter.

To return to the observations made at Plymouth. In *Sc. catulus* the amount of disturbance in the cloud of carmine, caused, as we have supposed, by the shutting of the spiracular valve, is greater than in the case of *Sc. canicula*. This was particularly noticeable in some experiments I made with a large Nursehound over 3 feet long.

RAJA.

The observations were made on fairly young specimens of *R. batis* measuring less than one foot from snout to tip of tail. The respiratory act in this fish is, in its main features, the same as in the Dogfish. In correspondence with the very much greater size of the spiracle and the greater differentiation of its valve (which has a serrated edge and is strengthened by the spiracular cartilage), the rapidity of the current and the volume of water drawn in at the spiracle is considerably greater than in *Scyllium*. Another difference between the two lies in the fact that when a Skate is resting he inhales water solely through his spiracle: it is only when he becomes restless and crawls or swims that water enters the mouth. A Skate clears his spiracle more forcibly and more often than a Dogfish does under the same treatment. A sleeping Dogfish will inhale suspended carmine for an indefinite time; but a sleeping *Raja* wakes and moves away after a very few trials with the carmine.

The existence of pigment on the anterior wall of the spiracle underneath the valve and the rich nerve-supply from the palatine branch of the 7th nerve to the spiracle itself, coupled with the above-mentioned facts relating to the respiratory current in this form, all point to the greater differentiation of the spiracle in the Ray than in *Scyllium*.

The observation of the exit of the water from the gills was not so easy a matter in the case of *Raja* as in that of the Dogfish. For, in the first place, *Raja* is much more easily made restless by the inhalation of carmine; and in the second, the water is not, so to speak, ejected directly to the exterior as in the case of the Dogfish, but to an intermediate closed chamber whose floor is the base of the vessel and whose roof and sides are the ventral surface of the fish. So far as I was able to observe, however, carmine liberated near the spiracle emerged chiefly from the foremost four gills; and, as in the Dogfish, carmine entering at the left side of the mouth emerged through the left gills, but also, though to a less extent, through the right ones.

The Ray occasionally did what I never observed *Scyllium* to do, namely, ejected water from the spiracle at each respiratory act for a considerable number of times. This regular and repeated reversal of the current in the spiracle was a very different thing from the occasional violent spasmodic expulsion of water, to which reference has already been made. The former barely disturbed the surface of the 2 inches of water in which the fish lay; the latter sometimes sent a spout of water half an inch from the surface.

It will be noted that in the foregoing account I have referred to that part of the anterior wall of the spiracle which moves backwards at each expiratory phase as the spiracular valve. I regard the behaviour of this structure sufficient justification for this name. But it must be pointed out that this valve is, certainly in the Ray, and, as far as I can discover, in the Dogfish too, identical with what is known as the pseudo-branch. It is not my intention to discuss the question whether this structure really represents a rudimentary gill or not: I am here merely concerned in pointing out the relation of its movements to the respiratory currents.

RHINA SQUATINA.

Rhina differs from both *Raja* and *Scyllium* in the following characters:—The mouth is terminal. The spiracle is much more elongate transversely even than in the Skate; it is, as shown in fig. 1, a considerable distance behind the eye; whereas in the Dogfish it is close behind it, and in the Ray it is even overlapped by the upstanding eye *. The spiracle possesses no valve. The gape of each gill-slit is much greater than is the case either in the Dogfish or the Skate. The gill-slits themselves appear crowded together in the postero-lateral angle of the pharyngeal region, as shown in fig. 2. This crowding is, however, only apparent, and is due to the great length of the gill-covers, and especially of the anterior ones, as shown in fig. 3.

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* The closeness of the eye to the spiracle in the Skate is the cause of a curious belief which, according to Dr. Masterman (to whom I am indebted for my acquaintance with it), exists among fishermen. They believe that the spiracle enables the fish to look into its pharynx and satisfy itself as to the quality of the food which it has swallowed.

The eye is certainly capable of a considerable degree of rotation.

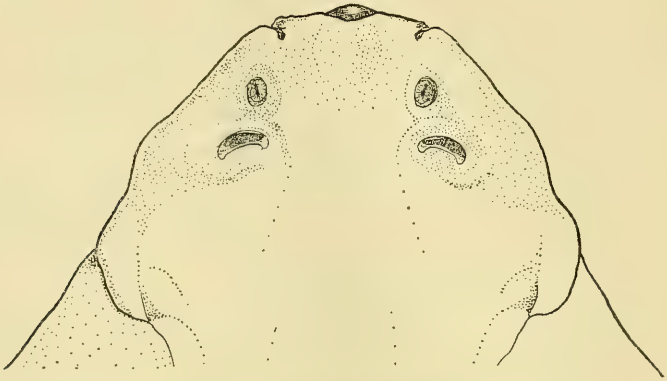

Fig. 1.—Dorsal view of Head and Pharyngeal Region of *Rhina*. ($\frac{3}{8}$ nat. size.)

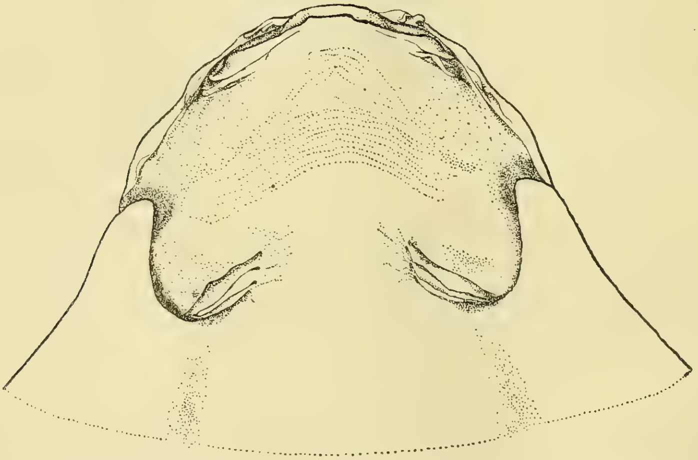

Fig. 2.—Ventral view of Head and Pharyngeal Region of *Rhina*. ($\frac{3}{8}$ nat. size.)

What strikes one most, when one looks at a living *Rhina* resting on the bottom of a tank or glass vessel, is its motionlessness. In a full-grown Angel-fish over 2 feet long, not only was there no trace of that regular heaving of the pharyngeal region which is so characteristic a feature of a resting Dogfish or Ray, but no movement of any kind in the anterior region of the body could be discerned. But in two younger Angel-fish the slightest signs of pulsation could be seen in the flaps of skin (fig. 1), which conceal the anterior extremities of the pectoral fins which can best be seen from below (fig. 2).

If we look a little closer, but still confine our examination to the upper and anterior part of the fish, we can see no sign of movement either in the spiracle or in the mouth, which is slightly open.

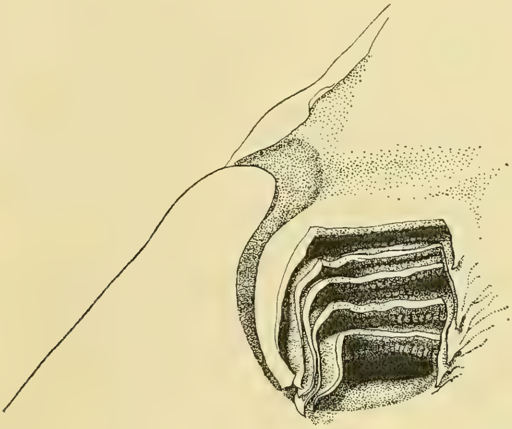

Fig. 3.—Ventral view of the postero-lateral angle of the pharyngeal region of *Rhina*, with part of the gill-covers cut away, to show their absolute and relative lengths. (About $\frac{5}{8}$ nat. size.)

It is not until we examine the ventral surface of the fish in the mirror that we can see any signs of movement, and even then we find the movement confined to the gill-covers themselves. The movement is expressed on the surface of the first gill-cover, and on as much of the others as can be seen, as a wave passing along it from its fixed anterior to its free posterior edge, and has very much the same appearance as a wave on a field of corn in the wind. There is absolutely no movement of the floor of the pharynx and still less that regular action of the floor which is so characteristic a feature of the living Dogfish, and (though to a less extent) of the Ray.

The list of differences between *Rhina* on the one hand, and *Scyllium* and *Raja* on the other, is not yet complete. Perhaps the most remarkable feature which distinguishes the Angel from the other fish examined is revealed by the experiments with carmine. Carmine liberated near the spiracle enters it in a *uniform stream*: that is to say, it is not drawn in rhythmically, as it is in the Dogfish and Ray, at each inspiration. In the case of the adult Angel the stream was perfectly uniform; in the case of two younger ones there was the faintest trace of pulsation, but this consisted merely in the slightest rhythmical acceleration of the current and not in the alternation of 'current' with 'no current.' Carmine liberated near the mouth entered it also in a uniform stream.

The uniformity of the stream is evidently due to the manner in which the respiratory current is brought about. It is effected by the undulation of the gill-covers, which expels the water underneath them to the exterior. Water enters the mouth and spiracles because these are the only channels through which it can enter the pharynx to replace that which has been expelled by the undulation of the gill-cover. The uniformity of the current is accounted for by the fact that by the time a wave has reached the hinder end of the gill-cover another has started at its anterior end.

It is evident how different is the method by which water is drawn in, in *Rhina* on the one hand and *Scyllium* and *Raja* on the other. For in these latter, as we have seen, this is effected by the expansion of the whole pharyngeal region accompanied by the simultaneous closing of the gill-slits and opening of the mouth and spiracle.

Water is drawn into the mouth and spiracle of *Rhina* in the same way as air is drawn into the door of a room which has a revolving ventilator in its roof. Water is drawn into these apertures in the Dogfish and Ray in the same way that smoke is drawn into the mouth from a tobacco-pipe or cigarette. In the first instance, the lumen of the chamber into which water (or air) is drawn is not enlarged; in the second, the lumen of the chamber into which water (or smoke) is drawn is enlarged.

We have said that when a living *Rhina* is examined no movement can be detected in the walls of the spiracle. The spiracle is, however, sometimes found open and sometimes shut; but from the fact that I have never seen the slightest movement on the part of the spiracle, although I examined it repeatedly whilst it was gradually but imperceptibly closing, I imagine that it never closes rapidly. In the case of the adult Angel which was examined in the large tank at Plymouth, the spiracle was always closed when the fish was undisturbed—for example, when I first visited it in the morning; but if it was disturbed and made to swim about, the spiracle gradually opened. But in the case of the two younger Angels which were confined to a shallow glass vessel in the laboratory in London, the spiracle was permanently open for a space of two days.

Judging the normal behaviour of the spiracle from the observations made in the large tank behind the Laboratory at Plymouth, we find that it is curiously different from that of the spiracle in the Ray. For whilst in the undisturbed Ray the water is drawn solely through the spiracle and not through the mouth at all, in the undisturbed Angel the spiracle is shut and water enters solely through the mouth.

The spiracle closes by the backward movement of its anterior border. This I was able to determine on a fish that had just died. One of the reflex movements executed as a result of pressing the back of the fish was the shutting of the spiracle, which was brought about in the manner described.

Summary of Results.

1. Water is drawn into the mouth and spiracle of the Dogfish by the expansion of the whole pharyngeal region. Water is prevented from entering the gill-slits by their automatic closure. The gill-covers are passive agents in determining the respiratory current.

2. The respiratory current in the Ray is brought about in essentially the same way as in the Dogfish.

3. The differences between the Dogfish and Ray in this respect all relate to the flat shape and bottom-living habit of the Ray. (*a*) In the former the greater part of the inhaled water enters through the mouth ; in the latter, through the spiracle, and indeed, when the fish is at rest, solely through the spiracle ; in the Dogfish, water never enters solely through the spiracle. (*b*) The Dogfish is capable of occasionally ejecting water from the spiracle ; the Ray can not only do this with much greater vehemence, but is capable of definitely reversing the current for a considerable number of respiratory acts. (*c*) In correspondence with the greater control which the Ray has over its spiracle, this aperture is both much larger than it is in the Dogfish and provided with a more efficient valve.

4. In *Rhina* the water is drawn into the mouth by an entirely different mechanism from that which obtains in the Dogfish and the Ray ; namely, by the undulation of the gill-covers themselves. The gill-covers in this fish therefore are active agents in determining the respiratory current. The current entering the mouth and spiracle is uniform and not rhythmical ; this is the result of the method by which the water is drawn in. The spiracle in *Rhina* is only capable of slow and imperceptible opening and closing ; it does not open and shut rhythmically, as in the case of the Ray and Dogfish.

5. The profound difference between the respiratory mechanism in *Rhina* on the one hand, and *Scyllium* and *Raja* on the other, makes strongly against the view, which Regan * opposes on anatomical grounds, that *Rhina* is a connecting link between the Sharks and Rays. At the same time, this mechanism in *Rhina* is as different from that in the Dogfish as it is from that in the Ray. Our attitude to the conclusion arrived at by Regan, that *Rhina* is a Shark and not a Ray, depends on the significance we attribute to physiological characters of this kind, in classification.

An abstract of this paper was read in the meeting of the Linnean Society. The experiments with carmine were demonstrated on two Rays, two Dogfish, and two Angel-fish, sent up from Plymouth for the occasion ; so that any of my statements which did not carry conviction could be immediately subjected to the test of experiment on the living animal. The only one of my propositions, which was objected to, was that which referred to the passivity of the gill-covers in the Dogfish as contrasted with the activity of these in *Rhina*. Prof. Herdman, who disclaimed familiarity with the behaviour of these structures in *Rhina*, said that from watching living dogfish on other occasions he had come to the conclusion that the gill-covers were not passive but active agents in determining the respiratory current. Dr. Masterman, however, was in agreement with the view which I had expressed. After looking into the matter again in the light of these criticisms, I have come to a conclusion which reconciles these two apparently opposite views. The anterior half of each gill-cover is supported by the gill-rays which are borne by the anterior four epibranchial cartilages. If we look at the living dogfish, we see that the anterior part of each gill-cover certainly does seem to move of its own accord, so to speak, and not merely as the result of the outgoing rush of water. Indeed, when we consider that the gill-rays, which support the anterior part of the gill-cover, are attached to the branchial cartilages to whose movement the expansion of the pharynx is largely if not wholly due, it is difficult to imagine that it could be otherwise. On the other hand, there can be no doubt that that part of the gill-cover which is not supported by the gill-rays is an absolutely passive agent and that its movements, like those of any valve, are solely determined by the direction of the current which plays upon it.

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* P. Z. S. 1906, p. 751.

Postscript.—After this paper had been sent to press, my attention was called to an article in the 'American Naturalist' (May 1907) by Herbert W. Rand, "On the Functions of the Spiracle in the Skate." I am happy to find that Mr. Rand's results, made on a species of *Raja* I have not examined, are in complete accord with those of my own which refer to the Skate.